Effects of Temperature and Season on Foraging Activity of Red Imported Fire Ants (Hymenoptera: Formicidae) in Oklahoma

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ABSTRACT Temperature and seasonal effects on foraging activity of *Solenopsis invicta* Buren (red imported fire ant) in Oklahoma were investigated by periodically quantifying the number of ants captured in baited vials for 2 yr. All temperature parameters (soil surface, 2 cm, 15 cm, mound surface, mound 5 cm deep, and mound 10 cm deep) except ambient at 1 m above soil surface were significant predictors of foraging activity; soil temperature at 15 cm was the best individual predictor, explaining 34% of variability in foraging activity. A combined quadratic model including mound surface temperature and season (weeks) explained 63% of the variability in foraging activity. Comparison with a similar study conducted in Florida revealed differences in the percentage of the year favorable for maximal foraging (≈25% in Oklahoma versus 42–59% in Florida). These data suggest that recommendations for timing of insecticidal bait applications against *S. invicta* that are appropriate in more southern portions of the fire ant range may not be appropriate for Oklahoma.

KEY WORDS *Solenopsis invicta*, temperature, foraging rates, bait

TEMPERATURE RELATIONS AND SEASONAL activity patterns of *Solenopsis invicta* Buren, the red imported fire ant, have been the subject of several studies, ranging from strictly applied experiments (e.g., Lofgren et al. 1964) to questions of physiology, growth, and energetics (e.g., Francke et al. 1986, Porter 1988, Calabi and Porter 1989, Porter and Tschinkel 1993, Tschinkel 1993, Vogt and Appel 2000). *Solenopsis invicta* populations may have undergone physiological changes resulting in greater desiccation tolerance as they moved into drier areas of the western United States (Phillips et al. 1996, Li and Heinz 1998). Evidence of adaptation to cool temperatures exists for at least one ant species (*Leptothorax acervorum* L.; Heinze et al. 1998). *Solenopsis invicta* may exhibit short-term adaptation to cold by depressing its supercooling point (Landry and Phillips 1996), but no evidence exists to indicate that populations of *S. invicta* are adapting to cooler temperatures as they move northward in the United States. Diffie et al. (1997) detected no difference in winter survival of hybrid imported fire ants (*S. invicta x richteri*) and *S. invicta* even though the hybrid form occurs north of *S. invicta.* Markin et al. (1974) observed differences in *S. invicta* activity in northern Mississippi compared with Florida populations, but

detected no difference in temperature thresholds for foraging activity between sites.

From a management standpoint, temperature and seasonal effects on foraging activity in *S. invicta* are of great interest. Bait products are currently the most effective means of controlling these pests over large areas, and efficacy depends on ant foraging activity. In Oklahoma, frequent complaints of early-season (≈April) control failures have led some consumers to lose confidence in bait products (W.A.S., personal observation). The most comprehensive study to date of temperature and seasonal effects on *S. invicta* foraging activity was performed in Florida (Porter and Tschinkel 1987). Foraging activity was driven primarily by soil temperature at 2 cm deep, with a slight drop in activity in the fall, which was unexplained by temperature. Ants foraged year-round, and by mid-March through April, mean foraging activity sometimes approached the predicted maximum for late June-early July. Soil temperature (2 cm deep) accounted for 59% of sample variation, and 78% of the variation was explained by a combined model of soil temperature (2 cm deep) and season. This study provided solid data for timing of bait applications to take advantage of high ant activity and modeled foraging activity for locations at several latitudes. Because soil temperature and season are linked, recommendations based upon season alone are likely to be misleading in other areas. Recent efforts to establish biological control organisms [e.g., *Pseudacteon* sp. (Diptera: Phoridae)] against *S. invicta*

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might benefit from increased knowledge of host activity patterns.

Area-specific data were needed to update and refine bait application recommendations for southern Oklahoma, where *S. invicta* have been present since ≈1985 (K. N. Pinkston, personal communication); thus, the primary objective of this study was to examine temperature and seasonal trends in foraging. We also compare foraging and temperature relationships with earlier work by Porter and Tschinkel (1987) to determine whether predictors of foraging activity in Florida apply to Oklahoma.

Materials and Methods

The study site was a power line right-of-way (≈30 m wide) located at Lakeside Recreational Area near Platter, Bryan Co., OK (33° 56′ 15″ N, 96° 33′ 02″ W). This site was characterized by mixed vegetation, evenly split in spring between forbs and grasses (e.g., Fleabane, alfalfa, bromes); by late summer, only forbs remained (e.g., *Lespedeza* sp., *Cassia* sp., and fogfruit). The site was clipped to ≈10 cm twice per year.

On each sampling day, 12, 60-ml snap-cap, semiopaque polypropylene vials, baited with a small amount of hotdog and grape jelly (≈0.5 g each) were placed on the soil surface at 7-m intervals along a trap line. A combination of materials (fats and proteins in the hotdog, carbohydrates in the jelly) was used because *S. invicta* exhibit seasonality in their attraction to carbohydrates and proteins (Stein et al. 1990). The vials were left open for 30 min then rapidly capped, collected, and returned to the laboratory for sorting and counting of trapped ants. Soil temperatures (surface, 2, and 15 cm deep), mound temperatures (surface, 5, and 10 cm deep), and ambient air temperature in shade (≈1 m above ground level) were recorded. Soil and mound temperatures were recorded in five random locations within the study area and averaged. Temperatures were taken with a digital thermometer (model KM45; Comark Limited, Welwyn Garden City, Hertfordshire, UK) equipped with a 76-cm thermocouple probe. General weather conditions (percent cloud cover, wind) were noted at the time of sampling. Sampling took place at 1- to 2-wk intervals from April 1999 through May 2001. During cold periods, if ants were not active (determined by direct observations and/or lack of response to placement of a small amount of hotdog on the soil surface), sampling was not done. Four samples included an additional set of six vials prepared exactly the same as above but shaded with small (≈10 × 10 cm) pieces of cardboard. Each shaded vial was paired with an unshaded vial (≈1 m away). Before collection, air temperatures within the vials were taken with a fine (0.3 mm dia.) thermocouple.

Vial size was not a limiting factor in our study (Porter and Tschinkel 1987); however, in a 30-min sampling period when ants were very active, foragers sometimes formed well-defined trails and removed a portion of the bait. Ant capture data did not directly reflect foraging activity in the environment surrounding the vials, but provided an index for comparison among temperatures.

Statistical Analysis. Data (mean number of foragers per vial) were $\log_{10}$-transformed and subjected to regression analysis to determine the best predictors of foraging activity using General Linear Models (SAS Institute 1985). Temperature and mean number of ants in shaded versus unshaded vials were compared using Analysis of Variance (SAS Institute 1985). Data are reported as mean ± SE.

Results

Temperature and Season. A quadratic model was fitted to log-transformed foraging data (mean number of *S. invicta*/vial) to determine the predictive value of various temperature measurements in individual regressions. Only data points with mean number of *S. invicta* per vial >10 were included in the analyses (N = 46). A thermocouple malfunction during two sampling runs resulted in a discrepancy in degrees of freedom for the analysis of seasonal effects (N = 45) and analyses including temperature (N = 43). One influential observation was omitted from the analyses; we mention it here because it is worth noting that foraging activity was documented (mean number of *S. invicta* per vial = 50.7 ± 2.4) when all soil temperatures were >42.6°C. On this occasion grass at the site was particularly tall (≈50 cm) and provided some shade for the vials.

All temperature parameters significantly influenced foraging activity ($P < 0.002$) with the exception of ambient temperature ($P = 0.14$). Soil temperature at 15 cm was the best predictor of foraging activity; even so, it only explained ≈34% of the variability for the model:

$\log_{10}$ *S. invicta* per vial =

$$-2.34 + 0.29 \text{ temperature} - 0.005 \text{ temperature}^2$$

(Table 1; Fig. 1). Soil (2 cm deep), mound surface, soil surface, mound 5 cm deep, and mound 10 cm deep explained 32, 30, 29, 26, and 24% of variability, respectively (Table 1; Fig. 1). Time of day (morning, afternoon, night) did not affect foraging activity ($P > 0.2$).

Season (expressed as weeks from 1 January) explained 49% of the variability in foraging in the model:

$$\log_{10} \text{ \emph{S. invicta} per vial} = -1.87 + 0.24 \text{ wk} - 0.004 \text{ wk}^2$$

($F = 19.5$, df = 2, 43, $P < 0.0001$) (Fig. 2). A model combining season and mound surface temperature explained 63% of the variability in foraging activity (Table 2):

$$\log_{10} \text{ \emph{S. invicta} per vial} = -3.36 + 0.16 \text{ temperature} - 0.003 \text{ temperature}^2 + 0.21 \text{ wk} - 0.003 \text{ wk}^2$$

Adding season to models for the other temperature measurements also resulted in increased precision.

To detect more subtle seasonal effects, residuals were obtained by solving for the various temperature measurements, and plotted versus season (Fig. 3) (e.g., Porter and Tschinkel 1987). Examination of the

Table 1. Regression coefficients and summary statistics for effects of various temperature measurements on *S. invicta* foraging activity in Oklahoma

Temperature	F	df	P	r^2	Coefficient ± SE		
					Intercept	Temperature	Temperature^2
Soil surface	8.6	2, 41	0.0008	0.2954	−3.34 ± 1.28	0.39 ± 0.10	−0.007 ± 0.002
Soil 2 cm	9.9	2, 41	0.0003	0.3245	−3.61 ± 1.36	0.40 ± 0.11	−0.007 ± 0.002
Soil 15 cm	10.6	2, 41	0.0002	0.3406	−2.34 ± 1.62	0.29 ± 0.14	−0.005 ± 0.003
Mound surface	8.9	2, 41	0.0006	0.3022	−1.80 ± 0.85	0.25 ± 0.06	−0.004 ± 0.001
Mound 5 cm	7.3	2, 41	0.0019	0.2625	−2.01 ± 1.03	0.27 ± 0.08	−0.004 ± 0.001
Mound 10 cm	6.3	2, 41	0.0041	0.2355	−1.83 ± 1.40	0.25 ± 0.11	−0.004 ± 0.002

residuals revealed seasonal trends not explained by temperature. Early and late in the season, all models tended to overestimate foraging activity, and during late summer months (August–September) they tended to underestimate foraging activity.

Shaded Versus Unshaded Vials. Temperature averaged 34.8 ± 0.7°C in shaded vials, and 37.4 ± 1.0°C in unshaded vials (NS, P = 0.07). The mean number of ants collected in shaded and unshaded vials was very similar (28.8 ± 7.9 versus 28.0 ± 9.0, respectively).
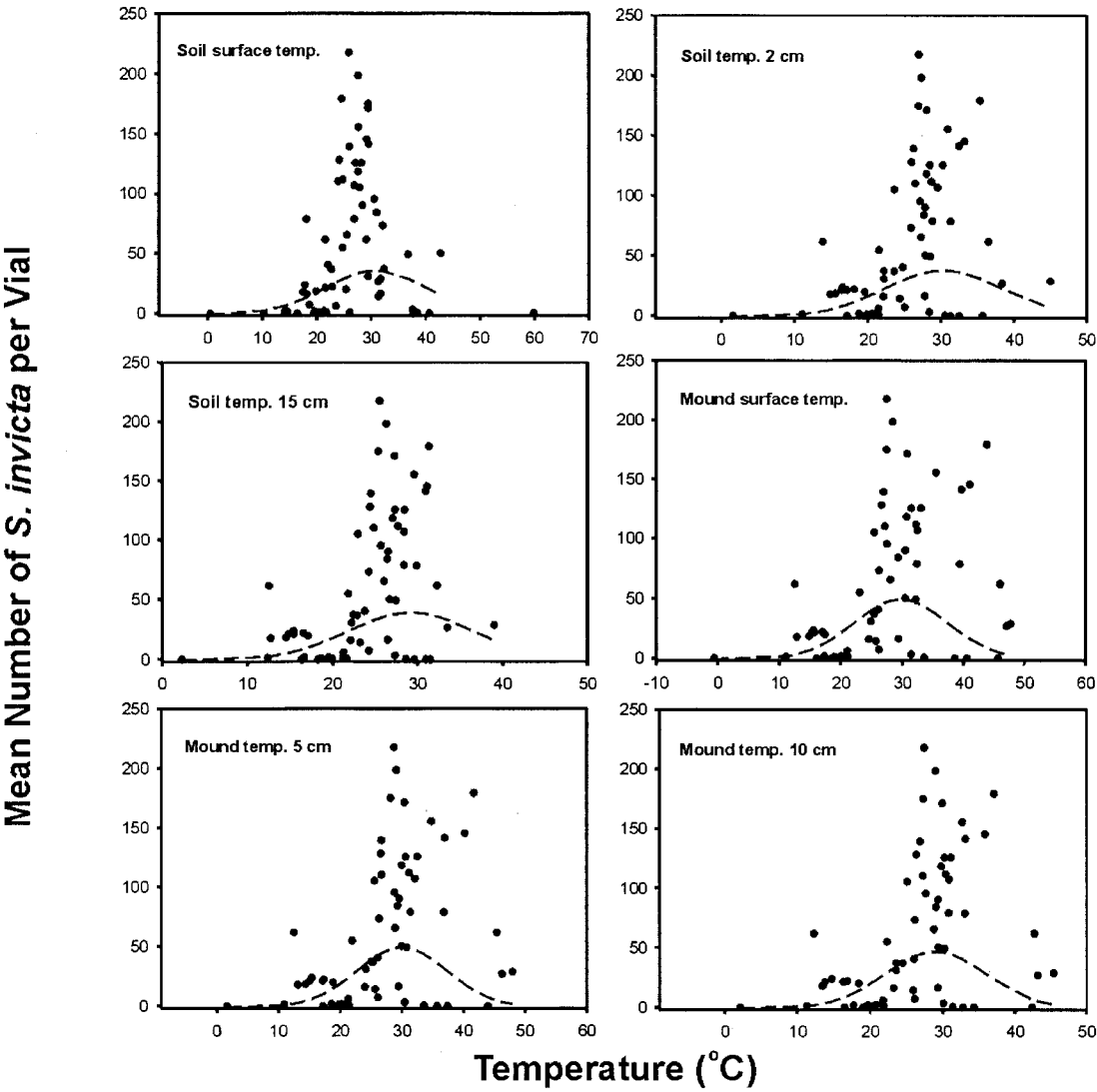

Fig. 1. Predictive value of several temperature measurements for foraging in *S. invicta*. Each point represents the mean number of *S. invicta* foragers captured per baited vial (N = 12) in a sample run. Dashed lines plot the regression of log$_{10}$-transformed data over the temperature parameters (Table 1).
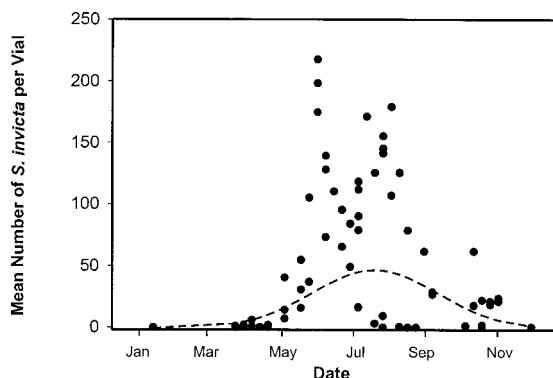
Fig. 2. Effect of season on *S. invicta* foraging activity in Oklahoma. Each point represents the mean number of *S. invicta* foragers captured per baited vial ($N = 12$) in a sample run. The dashed line plots the regression equation: Log_{10} *S. invicta* per vial $= -1.87 + 0.24\,\mathrm{wk} - 0.004\,\mathrm{wk}^2$ ($F = 19.5$, df $= 2, 43$, $P < 0.0001$).

Fig. 3. Effect of season on *S. invicta* foraging activity in Oklahoma after removing the effect of soil surface temperature. Removing the effect of other temperature measures and plotting residuals over season resulted in similar relationships.

Ambient temperature averaged $33.7 \pm 2.4°C$ during trial runs with shaded and unshaded vials, slightly lower than temperature in the vials.

Discussion

Season was the best individual predictor of foraging activity in our study. This contrasts with Porter and Tshinkel's (1987) study in which forager activity was best predicted using a model with soil temperature at 2 cm as the independent variable. In Florida, fire ants forage year-round, as long as temperatures are suitable for activity. In Oklahoma, foraging essentially ceased from mid December to mid March, and maximal foraging rates were not realized until June. Our temperature measurements were relatively poor predictors of foraging activity, accounting for 24–34% of the variability in activity (Fig. 1); however, no obvious differences exist between Oklahoma and Florida in the range of temperatures suitable for activity. Peak activity occurred at soil temperatures (2 cm deep) of $\approx 29°C$ in Oklahoma and Florida. Foraging tended to continue at higher temperatures in Porter and Tschinkel's (1987) study; however, they shaded their vials and we did not. Slightly higher temperature in unshaded vials (see Results) may have confounded our data, and direct comparisons are not appropriate. Other factors that could possibly influence tempera-
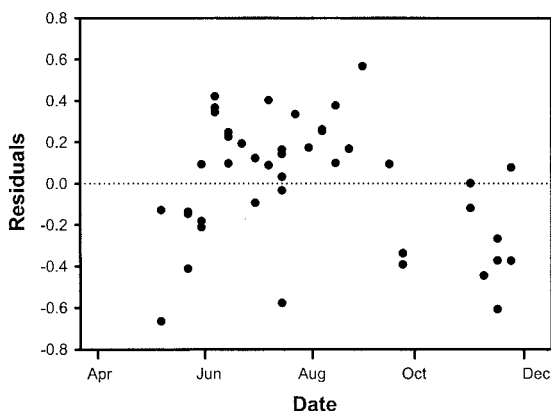
ture and foraging relationships include soil type, presence of other ant species (apparently not a factor at our site), and other weather phenomena. We did not sample within 24 h of a rain, so rainfall was not a factor in our study.

Unexplained variation in foraging activity during the season (Fig. 3) was similar to that observed in Florida (Porter and Tschinkel 1987), though overestimation of foraging activity in Oklahoma persisted for ≈ 7 mo and in Florida it persisted for ≈ 3 mo. Porter and Tschinkel (1987) hypothesized that the drop in foraging activity late in the season might be because of decreased preference for protein during winter months (e.g., Stein et al. 1990). Some other factor must be responsible for seasonal variation in foraging that is not explained by temperature, because we used a combination of high protein and high carbohydrate baits, and still observed lower foraging rates in fall and winter. During these months, a smaller percentage of foragers may meet the metabolic needs of colonies.

According to our data, $\approx 25\%$ of the year is favorable for maximal *S. invicta* foraging activity in open, grassy areas in southern Oklahoma (Fig. 2). This contrasts sharply with estimates published by Porter and Tschinkel (1987) for Georgia (36–47%), Mississippi (35–37%), central Alabama (36%), and Florida (42–59%). In our study, a combined model of mound surface temperature and season explained only 63% of the

Table 2. Regression coefficients and summary statistics for combined models of effects of season (weeks) and temperature on *S. invicta* foraging activity

Temperature	F	df	P	r^2	Coefficient $\pm$ SE				
					Intercept	Temperature	Temperature^2	Weeks	Weeks^2
Soil surface	15.9	4, 39	<0.0001	0.6205	-5.06 ± 1.16	0.27 ± 0.08	-0.005 ± 0.002	0.24 ± 0.05	-0.004 ± 0.001
Soil 2 cm	12.1	4, 39	<0.0001	0.5533	-4.38 ± 1.34	0.22 ± 0.10	-0.004 ± 0.002	0.23 ± 0.05	-0.004 ± 0.001
Soil 15 cm	10.0	4, 39	<0.0001	0.5060	-4.01 ± 1.95	0.16 ± 0.14	-0.003 ± 0.003	0.26 ± 0.08	-0.004 ± 0.001
Mound surface	16.4	4, 39	<0.0001	0.6266	-3.36 ± 0.86	0.16 ± 0.05	-0.003 ± 0.001	0.21 ± 0.05	-0.003 ± 0.001
Mound 5 cm	13.2	4, 39	<0.0001	0.5747	-3.62 ± 1.02	0.16 ± 0.06	-0.003 ± 0.001	0.23 ± 0.05	-0.004 ± 0.001
Mound 10 cm	10.2	4, 39	<0.0001	0.5104	-3.31 ± 1.39	0.11 ± 0.10	-0.002 ± 0.002	0.25 ± 0.06	-0.004 ± 0.001

variation in foraging activity. Activity data exhibit a high degree of scatter (Fig. 1); thus, temperature and season should not be used alone to predict optimal foraging. Additionally, other habitat types may exhibit different microclimate variation on a scale of hours or seasons, affecting fire ant foraging activity. Our data do not suggest adaptation by *S. invicta* to cooler temperatures in the northern part of its range. Detailed physiological studies might shed light on whether populations of *S. invicta* in Oklahoma differ appreciably from populations in more southern areas.

This study highlights the importance of carefully timing bait applications for maximal foraging activity, and helps explain early-season control failures in Oklahoma. Current control recommendations for fire ants in Oklahoma include monitoring for fire ant activity before baiting by placing small bits of an attractive substance (for example, greasy potato chips, hotdog slices, peanut butter) on the ground in several places within the area to be treated and checking the material for foraging ants. If ants discover and recruit to the food sources within 20–30 min, bait may be broadcast over the area. Seasonal control recommendations that are appropriate for other areas in the United States (e.g., April through June in Texas (http://www.fireant.tamu.edu/springflyer.pdf) are not appropriate for more northern areas of infestation. Release of biological control agents that parasitize fire ants exposed on the ground (e.g., decapitating flies, *Pseudacteon* sp.; Diptera: Phoridae) should take place during June through August in Oklahoma.

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